1   Short Title: Tracking and forecasting community state

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3   **Tracking and forecasting community responses to climate perturbations in the California**

4   **Current Ecosystem**

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Abstract

Ocean ecosystems are vulnerable to climate-driven perturbations, which are increasing in frequency and can have profound effects on marine social-ecological systems. Thus, there is an urgency to develop tools that can detect the response of ecosystem components to these perturbations as early as possible. We used Bayesian Dynamic Factor Analysis (DFA) to develop a community state indicator for the California Current Ecosystem (CCE) to track the system's response to climate perturbations, and to forecast future changes in community state. Our key objectives were to (1) summarize environmental and biological variability in the southern and central regions of the CCE during a recent and unprecedented marine heatwave in the northeast Pacific Ocean (2014–2016) and compare these patterns to past variability, (2) examine whether there is evidence of a shift in the community to a new state in response to the heatwave, (3) identify relationships between community variability and climate variables; and (4) test our ability to create one-year ahead forecasts of individual species responses and the broader community response based on ocean conditions. Our analysis detected a community response to the marine heatwave, although it did not exceed normal variability over the past six decades (1951-2017), and we did not find evidence of a shift to a new community state. We found that nitrate flux through the base of the mixed layer exhibited the strongest relationship with species and community-level responses. Furthermore, we demonstrated skill in creating forecasts of species responses and community state based on estimates of nitrate flux. Our indicator and forecasts of community state show promise as tools for informing ecosystem-based and climate-ready fisheries management in the CCE. Our modeling framework is also widely applicable to other ecosystems where scientists and managers are faced with the challenge of managing and protecting living marine resources in a rapidly changing climate.

Introduction

Climate perturbations can have strong impacts on ocean ecosystems that in turn affect social and economic components of human communities. These effects may be exacerbated when changes in ocean conditions are more extreme, such as during marine heatwaves. The increasing attention on these extreme events and their impacts (e.g., Hobday et al. 2018, Sen Gupta et al. 2020) has invigorated a push for tools that can track and detect as early as possible the response of marine communities to climate-driven perturbations. Early detection, and moreover, near-term forecasts of community shifts could help scientists, managers, and stakeholders better prepare for and respond to the potential consequences of such shifts.

Climate-driven shifts in community structure tend to involve rapid change across multiple populations that result in switches between contrasting community assemblages that may then persist for decades. A growing number of studies have documented community reorganizations in response to climate drivers (e.g., Beaugrand et al. 2008, 2015, Möllman and Diekmann 2012, Wernberg et al. 2016, Peabody et al. 2018). One of the best-known examples is the widespread northeast Pacific community reorganization that followed the 1976/1977 shift in the Pacific Decadal Oscillation (Benson and Trites 2002; Hare and Mantua 2000). The abrupt change from a cool to warm ocean regime had dramatic implications on ecosystem functioning and living marine resources (LMRs) throughout the region (Mantua et al. 1997, Anderson and Piatt 1999; Litzow and Ciannelli 2007, Peabody et al. 2018). Since then, northeast Pacific marine ecosystems have experienced several interannual or decadal perturbations that do not appear to have resulted in community-wide shifts of similar magnitude. However, between 2014 and 2016 these ecosystems experienced a marine heatwave that involved the warmest sea surface temperature (SST) and heat content anomalies that had ever been observed over large areas of

82   the North Pacific (Bond et al. 2015; Walsh et al. 2018). It was one of the most extreme

83   heatwaves globally in its combined magnitude, spatial scale, and duration (Hobday et al. 2018,

84   Sen Gupta et al. 2020), and the intense, persistent warming has been attributed to a combination

85   of natural and anthropogenic forcing (Jacox et al. 2018a; Laufkötter et al. 2020).

86   Several studies have documented myriad biological responses to this event. For example,

87   within the California Current Ecosystem (CCE), there were mass strandings of marine mammals

88   (Cavole et al. 2016), increased whale entanglements due to shifting prey sources (Santora et al.

89   2020), mass mortality events for marine seabirds (Cavole et al. 2016, Jones et al. 2018, Piatt et

90   al. 2020), a record-breaking domoic acid outbreak (McCabe et al. 2016), shifts in pelagic

91   macronekton and micronekton communities and species richness (Santora et al. 2017, Brodeur et

92   al. 2019, Nielsen et al. 2020), irruptions of previously rare fishes and invertebrates throughout

93   the California Current (Sakuma et al. 2016, Morgan et al. 2019, Sanford et al. 2019, Walker et al.

94   2020), and extraordinarily high recruitment of rockfishes (genus *Sebastes*; Schroeder et al. 2018,

95   Field et al. 2021) and northern anchovy (*Engraulis mordax*; Thompson et al. 2019). Yet, to date,

96   there have been few quantitative studies of how the marine heatwave impacted the broader CCE

97   community at multiple trophic levels, and therefore the importance of this extreme event for

98   community-wide patterns of variability, and the persistence of the community response, remains

99   largely unknown.

100   Indicators of community or ecosystem state are valuable tools for tracking climate-related

101   changes in ecosystem functioning and evaluating those changes within the context of past

102   climate perturbations (Harvey et al. 2020). Moreover, combining long-term monitoring surveys

103   and data with modeling frameworks that summarize information across taxa and life stages that

104   respond quickly to climate perturbations could provide early detection of an ecosystem shifting

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105   into a novel state. Early detection of such shifts would benefit ecosystem-based and climate-

106   ready fisheries management strategies aimed at mitigating possible deleterious ecological and

107   socio-economic outcomes. There is also a pressing need for forecasts of future ecosystem states

108   to support forward-looking management of LMRs (Hobday et al. 2016, Tommasi et al. 2017,

109   Jacox et al. 2020), including assessments of risk. As climate models and forecasts of ocean

110   conditions continue to improve, the time is ripe for developing and testing methods that could

111   provide near-term forecasts of community state in relation to ocean conditions.

112   A challenge in summarizing ecosystem responses to perturbations is that time series used

113   to characterize the ecosystem often involve tens to hundreds of variables (species or climate

114   indices); there is often some degree of asynchrony among time series, and further, each is

115   corrupted by the presence of observation errors. Disentangling these sources of error and

116   separating the signal from the noise is statistically challenging. Traditionally, tools such as

117   Principal Components Analysis (PCA) or nonmetric multidimensional scaling have often been

118   used for identifying leading patterns of variability in multivariate datasets (e.g., Koslow et al.

119   2002, 2013); however, these approaches are ill-suited to the analysis of time series data that are

120   autocorrelated or non-stationary (Planque and Arneberg 2018). An alternative approach,

121   Dynamic Factor Analysis (DFA), is better suited for identifying shared trends that can be used as

122   a community state indicator. DFA is specifically designed for time series ordination, and avoids

123   many of the problems associated with other multi-variate approaches (Zuur et al. 2003). When

124   applied to a collection of multivariate time series, inference in DFA models focuses on

125   estimating a smaller number of temporal patterns ('trends') that best capture the variation

126   observed. The observed data are then treated as a mixture of these trends (Ward et al. 2019).

127   Ward et al. (2019) recently developed a Bayesian implementation of DFA that models shared

128   trends, detects "black swan" events (rare and difficult to predict events; Anderson et al. 2017),

129   and estimates the probability of switches among contrasting system states. In the first application

130   of this new method, Litzow et al. (2020a) examined shared trends of climate and biology time

131   series in the Gulf of Alaska. Their study did not detect evidence for wholesale community

132   reorganization during the recent northeast Pacific marine heatwave; however, their findings

133   indicated potential for new patterns of ecosystem functioning with continued warming of ocean

134   temperatures.

135   Here we build on this set of novel statistical tools to develop a model of the CCE state

136   that can both track and forecast ecosystem changes in response to climate perturbations.

137   Specifically, we expand the Bayesian implementation of DFA to test the community response to

138   environmental variables within the modeling framework and to develop near-term forecasts of

139   future community states. Using climate and biological data from the central and southern regions

140   of the CCE, our goals were to: (1) summarize environmental and biological variability during

141   2014–2016 and compare these patterns to past variability; (2) assess the probability of observed

142   departures from previous climate patterns and of switches to new states in community variability

143   during the heatwave; (3) identify relationships, if any, between community variability and

144   climate variables; and (4) test our ability to create one-year ahead simultaneous forecasts of

145   species responses and the community state based on environmental information. While the focus

146   of our study is the CCE, the approach applied here is widely applicable to the myriad marine

147   ecosystems worldwide that are vulnerable to a rapidly changing climate.

148

149   **Methods**

150   *Data*

151   In our analysis, we used oceanographic time series from the southern (n=6) and

152   central (n=6) regions of the CCE, derived from a data assimilative configuration of the Regional

153   Ocean Modeling System (ROMS) with 0.1˚ (~10 km) horizontal resolution and 42 terrain-

154   following vertical levels (Neveu et al. 2016; oceanmodeling.ucsc.edu). From the ROMS output,

155   we generated monthly time series covering 1980-2018 for a suite of variables including sea

156   surface temperature (SST), sea surface height (SSH), isothermal layer depth (ILD), Brunt-

157   Väisälä frequency (BV), a coastal upwelling transport index (CUTI), and a biologically effective

158   upwelling transport index (BEUTI). The ILD is similar to mixed layer depth and defines the

159   depth where temperature deviates by 0.5˚C from the surface value. BV is a measure of water

160   column stratification, averaged over the upper 200 m of the water column. CUTI and BEUTI are

161   upwelling indices that quantify vertical transport and nitrate flux through the base of the mixed

162   layer, respectively (Jacox et al. 2018b). The data were annually averaged (July-June) from the

163   coast to 100 km offshore, with the exception of CUTI and BEUTI, which capture coastal

164   upwelling within 75 km of shore. In the alongshore direction, we calculated averages for two

165   regions with a division at Point Conception, California, separating the southern portion of the

166   CCE (31–34.5˚N) from the central region (34.5-40.5˚N, Fig. 1). The annual averages were taken

167   from July to June to capture the influence of the El Niño–Southern Oscillation (ENSO), which

168   peaks in winter and is the dominant mode of interannual variability influencing the California

169   Current. We developed models using ROMS output rather than empirical measurements because

170   they provide full spatial and temporal coverage of surface and subsurface conditions, incorporate

171   available observations, and will enable the use of ROMS forecasts to then forecast biological

172   changes in the CCE. More details on the oceanographic time series can be found in S1 Table and

173   S1 Figure.

174

Figure 1. Sampling locations of California Current Ecosystem biology included in the study

analyses. Abundance data for pelagic juvenile groundfishes and invertebrates are collected on the

Rockfish Recruitment and Ecosystem Assessment Survey (RREAS). Ichthyoplankton data are

collected on the California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey.

Seabird reproductive success and California sea lion (*Zalophus californianus*) pup time series are

collected on Southeast Farallon Island and San Miguel Island, respectively. See S1 Table and S1

Figure for detailed information on the individual time series.

182

The biology time series included in our analysis were selected based on three criteria:

first, the measured variables would be expected to show rapid (0- to 1-year lag) responses to

climate variability; second, the time series could be updated with no more than one year lag for

processing time to increase the speed at which biological responses to perturbation could be

detected; and third, the time series were at least 15 years long. The biology time series that met

these criteria (n=38) included ichthyoplankton, pelagic young-of-the-year (juvenile fish), squid,

and krill abundance; seabird productivity; and California sea lion pup body condition metrics

(Fig. 1, S1 Table). These 38 time series were collected from four disparate ocean surveys, and

span between 22 and 68 years. Datasets collected from surveys that included spatial attributes

(e.g., ichthyoplankton and pelagic juvenile fish surveys) were first standardized using

Generalized Additive Models to create a univariate time series for each species. While these

datasets generally include spatial random sampling, the index standardization accounts for

uneven distributions of effort (in space or time). Details on the standardization of individual

datasets are included in S1 Appendix. In addition, the biology data were normalized with log

197   transformations where appropriate (all zeros were changed to NAs). For example, if the time

198   series data were assumed to be lognormally distributed (e.g., weight/count data) or the

199   coefficient of variation was > 1, the data were log transformed. All of the time series from an

200   individual dataset (survey) were treated the same, i.e., logged or not. More details on the biology

201   time series used in this study and the associated data sources and log transformations are

202   summarized in S1 Table and S1 Figure.

203

204   *Modeling*

205   We describe the methods in detail below, but in summary our work flow was to (1) apply

206   Bayesian DFA to climate and biology datasets separately and use model selection tools to

207   identify the best supported model and number of shared trends, (2) apply 'black swan' and

208   regime detection methods to detect extreme events and alternating community states,

209   respectively, (3) identify whether the CCE community state was strongly correlated with the

210   climate time series (compare performance of the biology models with/without environmental

211   covariates), and (4) evaluate our skill at making predictions of community state and individual

212   species variables.

213

214   *Dynamic Factor Analysis*

215   We used a Bayesian version of Dynamic Factor Analysis (DFA, Zuur et al. 2003, Ward et

216   al. 2019) using the software Stan and R (R Core Team 2018) as implemented in the 'bayesdfa'

217   package (Ward et al. 2020). DFA is a multivariate statistical tool somewhat analogous to

218   Principal Components Analyses, but for time-series data (Holmes et al. 2018, https://cran.r-

219   project.org/web/packages/MARSS/vignettes/UserGuide.pdf). For a collection of time series, the

220   number of estimated 'trends' is specified *a priori*, and DFA estimates these latent trends as

221   independent random walks. In mathematical form, this is expressed as

222    $$x_t = x_{t-1} + w_{t-1},$$

223   where x_t represents the value of latent (unobserved) trends at time t, and the process error

224   deviations w_{t-1} are generally assumed to be white noise having arisen from a multivariate

225   normal distribution (with an identity covariance matrix for identifiability). The latent trends are

226   mapped to the observed data through an estimated loadings matrix $\mathbf{Z}$ and residual error e_t,

227    $$y_t = \mathbf{Z}x_t + b \cdot d_t + e_t,$$

228   where y_t is the vector of observed states at time t, and the residual error terms e_t are assumed to

229   be drawn from a univariate or multivariate normal distribution. Though the covariance matrix of

230   w_t is generally fixed (Zuur et al. 2003), the covariance matrix of e_t can be structured; variances

231   may be shared or not across time series, and off diagonal elements may be estimated. The

232   parameter vector $\mathbf{b}$ represents optional estimated coefficients relating covariates d_t to the

233   observed response. In the context of our DFA modeling, we included climate variables as d_t in

234   models where the biological observations were used as the response y_t.

235   Because we implemented the DFA model in a Bayesian setting, we were able to extend

236   this model to include additional features. First, to include extreme events, we relaxed the

237   assumption about process errors w_t being drawn from a normal distribution and used a

238   multivariate Student-t distribution instead (Anderson and Ward 2019). We also modified the

239   process equation to consider an optional vector of AR(1) coefficients ϕ on the latent trends.

240    $x_t = \phi x_{t-1} + w_{t-1}$ (Ward et al. 2019). A final modification of the conventional DFA model is

241   that for some models, process variances can be estimated rather than fixed at 1 (maximum

242   likelihood approaches generally use this constraint for identifiability). As implemented in Stan

243   (Stan Development Team 2016, Hoffman and Gelman 2014, Carpenter et al. 2017), we

244   conducted estimation with three chains, with a warm-up of 2000 samples, followed by 2000

245   iterations. We used the split-chain potential scale reduction factor (Gelman and Rubin 1992,

246   Gelman et al. 2013) to assess convergence (Rhat < 1.05). Code to replicate these analyses is

247   deployed as an R package on CRAN ('bayesdfa', Ward et al. 2020) and our public Github

248   repository, https://github.com/fate-ewi/bayesdfa.

249   We ran the DFA on climate datasets (1981–2017) and biological datasets (1951–2017)

250   across the southern and central regions of the California Current combined. Running the analysis

251   at this spatial scale allowed us to capture the broader community response to climate

252   perturbations, compared to running models on each multivariate dataset independently (e.g., time

253   series from a single survey). There are a number of ways to evaluate predictive accuracy of these

254   models. Leave-One-Out Cross-Validation (LOO-CV), for example holds each observation out in

255   turn and predictions are made from the remaining data. As our focus was on the temporal nature

256   of the data and forecasting component, we implemented a variant of k-fold cross validation and

257   treated individual years as unique 'folds'. Because our objectives involved evaluating these

258   models for future predictions, we implemented the Leave-Future-Out Cross Validation

259   Information Criterion (LFO-CV, Bürkner et al. 2020). We used this approach to identify data

260   support for (1) the number of latent DFA trends (n = 1-3), (2) first-order autoregressive AR(1)

261   coefficients on the trends (ϕ estimated with a Normal(0,1) prior), (3) Student-t deviations (i.e.,

262   evidence of extreme events, using a prior on the MVT degrees of freedom parameter, ν, of $\nu \sim$

263   Gamma(2, 0.1)), and (4) a fixed versus estimated trend variance (using a prior on the standard

264   deviation, σ_w, of $\sigma_w \sim$ Normal(0,1)).

265   In addition, we used LFO-CV to identify the most appropriate error structure for the

266   climate dataset—specifically whether the times series had equal (shared) or unequal (unique)

267   observation errors. For the biology models, we assumed the observation errors were unique by

268   dataset, and our estimates of survey variance supported this assumption.

269   For each model formulation, we applied the LFO-CV method by first fitting the model to

270   all years of data prior to year T (i.e., training data) and then using the fitted model to predict the

271   trend value in year T (i.e., test data). We repeated this process for 10 years, starting with 2017 as

272   year T and working back to 2008, and then calculated the expected log predictive density

273   (ELPD) across those time steps. The climate and biology models with the highest ELPD were

274   deemed the best supported models. The LFO-CV is a preferred method for evaluating future

275   predictive performance of Bayesian models because it properly accounts for time series

276   structure, and unlike other Bayesian cross-validation methods, does not produce overly

277   optimistic estimates (Bürkner et al. 2020).

278

279   *Detection of extreme events and regime shifts*

280   After identifying the best-supported DFA model for the climate and biological datasets,

281   we conducted a post-hoc examination of outlier detection and regime shifts. For outlier detection

282   of black swan events, we implemented a method similar to that described in Anderson et al.

283   (2017) and applied it to the climate and biology time series. This approach relies on first

284   differencing the posterior trend mean estimates of the climate and biology trends, $x_t - x_{t-1}$ and

285   then applies a normal density function to identify year-over-year changes that were unlikely to

286   have arisen from a normal distribution (given the process variance). Probabilities can then be

287   assigned to the deviations in each year (e.g., 'there is a 1:1000 chance of observing a deviation

288 similar to that estimated in year *t'*). As described in Ward et al. (2019), the presence of regimes

289 can also be estimated by applying hidden Markov models (HMM) to the estimated state indices

290 from a DFA. We evaluated support for regimes and alternate states by using the posterior trend

291 estimates from each model as input. The Bayesian Leave-One-Out cross validation Information

292 Criterion (LOOIC, Vehtari et al. 2017) was used to identify the data support for the number of

293 trends (n = 1–3).

294

295 *Forecasting community state*

296 While a wide variety of multivariate or univariate time series methods could be applied to our

297 observed time series to generate forecasts, our objectives were to develop simultaneous estimates

298 of both the community state(s) and the raw time series. We evaluated the ability of our DFA

299 models to generate short-term (one year lead-time) forecasts of community state by first

300 evaluating whether the performance of the biology DFA model was improved when climate time

301 series were included as covariates in the model. If climate time series were found to better

302 explain the variability in the biology time series, these relationships could potentially be used to

303 forecast community trends. For our analysis, we ran the DFA on a subset of the biology data

304 overlapping in time with the climate dataset, i.e., 1981–2017, to make out-of-sample predictions.

305 We used the same LFO-CV procedure described above, with the same forecast period (2009–

306 2017) to compare the biology models with and without a single climate covariate (see S2 Table

307 for all model formulations). In this case, the model used biological and climate data from all

308 preceding years and climate data from the year to be forecast. The six climate covariates from

309 the southern region and the central region of the CCE (12 total) were tested in this analysis. Once

310 the best-supported biology-covariate model was identified, we used that model to make

311 predictions of individual species parameters and the community state in 2018 using climate data

312 from that same year. We evaluated forecast skill based on the prediction errors of individual

313 species parameters and by comparing the forecasts for 2009–2018 to the 2009–2018 trend values

314 estimated from biology-covariate model that only included data prior to the forecast year.

315

316 **Results**

317 *Climate and biology trends*

318 The model with the highest predictive accuracy (ELPD) of the climate state in the southern and

319 central regions of the CCE was a one-trend DFA model (Model 1 in Table 1, Fig. 2a). This

320 model included unique observation variances across the six time series, support for heavy-tailed

321 deviations of the latent trend, an AR(1) coefficient on the trend (S1 Fig.), and an estimated trend

322 variance. All but one of the climate time series (central ILD) were associated with the single

323 trend, i.e., at least 90% of the loading posterior distributions associated with each time series

324 were above or below zero (Fig. 2b). The SST, SSH, and BV frequency (water column

325 stratification) time series from the southern and central regions of the CCE loaded positively on

326 this trend (Fig. 2b). The BEUTI and CUTI time series from both regions of the CCE and the ILD

327 time series from the central region loaded negatively on the trend (Fig. 2b). Overall, the trend

328 captured a well-documented cooling period in the CCE between 1980 and 2010 (e.g., Seo et al.

329 2012), as well as strong El Niño events (e.g., 1982–1983, 1997–1998, 2015–2016) and the 2014–

330 2016 marine heatwave. The trends and loadings indicate that these events were generally

331 associated with weaker upwelling, reduced mixed layer depth, low nutrient flux, and warm,

332 stratified waters (Fig. 2a, b).

333

334 **Table 1.** Summary information for climate and biology Bayesian DFA models, including

335 whether process error was estimated, observation error variances (unequal or equal among time

336 series, or unique to each survey), the number of model trends, expected log pointwise predictive

337 densities (ELPD), and standard error of ELPD. Bold text highlights the models that show best

338 support or highest predictive accuracy for the climate and biology data for the southern and

339 central California Current ecosystem (i.e., highest ELPD). All climate and biology models

340 include an AR(1) process and Student-t deviations.

Time series	Model	Process sigma	Variance index	Trends	ELPD	SE ELPD
Climate	1	Yes	unequal	1	**-10551.89**	759.44
	2	No	unequal	1	-10682.39	712.96
	3	Yes	equal	1	-16793.59	1732.54
	4	No	equal	1	-16881.03	1824.42
	5	No	unequal	2	-17441.01	1655.23
	6	Yes	unequal	2	-17818.86	1813.65
	7	Yes	unequal	3	-21571.65	1674.77
	8	No	unequal	3	-22882.99	1695.12
	9	No	equal	2	-23927.86	2694.72
	10	Yes	equal	2	-24536.19	2953.38
	11	Yes	equal	3	-38895.66	4024.93
	12	No	equal	3	-38920.87	4762.15
Biology	13	No	survey	1	**-2003.32**	95.76
	14	Yes	survey	1	**-2003.96**	88.88
	15	No	survey	2	-2155.52	76.05
	16	Yes	survey	2	-2198.79	78.86
	17	No	survey	3	-2334.55	118.31
	18	Yes	survey	3	-2335.10	112.70

341

342

343 **Figure 2.** Climate variability in southern and central California Current ecosystem: a) shared

344 trend with 95% credible intervals (1981–2017), b) posterior distributions for loadings on all of

345 the individual time series. Loadings with darker shading indicate time series loading most

346 strongly on the climate trend. SST, sea surface temperature; SSH, sea surface height; ILD,

347 isothermal layer depth; BV, Brunt-Väisälä frequency (stratification); CUTI, Coastal Upwelling

348   Transport Index; BEUTI, Biologically Effective Upwelling Transport Index. See S1 Table and

349   S1 Figure for climate times series details.

350

351   The climate state during the marine heatwave, as indicated by the DFA trend, was within

352   the bounds of previous observations. While there was support in the best model for heavy-tailed

353   deviations in the climate trend (i.e., Student-t deviations S1 Fig.), our post-hoc examination of

354   outliers detected a single extreme event in the climate state in mid-1998 to mid-1999

355   (threshold=0.001), when there was a shift from strong El Niño (1997–98) to strong La Niña

356   (1998–1999) conditions, and not around the time of the heatwave. Application of the Bayesian

357   HMM to the climate trend most supported the presence of two hidden states, reflecting the

358   probability of being in a state associated with warmer conditions versus one with cooler

359   conditions (LOOIC: one-state = 129.1, two-state = 9.4, three-state = 27.2, Fig. 3). The LOOIC

360   did not provide support for a shift to a third novel climate state in the southern and central

361   regions of the CCE during the marine heatwave, however there is a shift back to the previously

362   observed warm state during the marine heatwave.

363

364   **Figure 3.** Results of Hidden Markov Models (HMM) showing state probability for latent trends

365   in the climate (top) and biology (bottom) data sets. The best model for both data sets invoked

366   two states, and the median probability (and 95% credible intervals) of being in one state versus

367   the other is shown. The top figure reflects the probability of being in the state associated with

368   warmer conditions versus one with cold conditions, and bottom figure indicates that ecosystem

369   did not shift into a new state following the marine heatwave.

370

371   The best model for community variability among our biological time series was also a

372   one trend model (Model 13 in Table 1, Fig. 4a). The model formulation was similar to the best

373   climate model, except the observation variances were unique by dataset (survey) and not

374   individual time series. We note that the top two models (Model 13 and 14) showed similar

375   predictive accuracy (Δ ELPD < 1) and only differed with respect to whether the process variance

376   was fixed at 1 or estimated. Here we only show results for the model with a fixed process

377   variance. The biology showed strong coherence in community signal; a majority of the time

378   series (31 of 38) loaded strongly (probability > 0.9) on the single trend and most of them

379   demonstrated loadings in the same direction (Fig. 4b). The magnitude and direction of the

380   estimated loadings were consistent with the observed high relative abundance of most juvenile

381   groundfishes (rockfish, flatfish), squid, krill, and some ichthyoplankton species increased during

382   the marine heatwave, and suggest that the reproductive success of some seabird species was

383   higher around the time of the heatwave as well. The few time series loading in the other direction

384   on the trend indicated a reduction in sea lion pup growth rate and lower abundances of

385   juvenile/adult Pacific sardine *Sardinops sagax* and some ichthyoplankton species (e.g., larval

386   northern anchovy and Pacific hake *Merluccius productus*) associated with the heatwave.

387

388   **Figure 4.** Community variability in the southern California Current ecosystem: a) shared trend

389   with 95% credible intervals (1951–2018), b) posterior distributions for loadings on individual

390   time series (only time series with ≥ 90% of the loading distributions above or below zero are

391   shown). Loadings with darker shading indicate time series loading most strongly on the biology

392   trend. Cal. = California, Juv. = juvenile fish stage, Juv./adult = juvenile and adult fish stages

393   combined, all other fish are larval fish. See S1 Table and S1 Figure for times series details.

394

395 The estimated trend from this biology DFA model demonstrates a potential shift in community

396 state in the mid-1960s, although there is considerable uncertainty around the trend during this

397 early portion of the time series, likely due to the limited number of observations

398 (ichthyoplankton only) pre-dating the 1970s (Fig. 4a, S1 Fig.). Similarly, the limited number of

399 biological time series and missing sampling years in the late 1960s and 1970s, and the lack of

400 climate outputs from ROMS prior to 1980, make it difficult to detect a documented transition

401 that happened in the mid-1970s (S1 Fig., see discussion). The community state appears to be

402 relatively stable from the late 1970s through the early 2000s, and the trend reached a peak

403 around 2013–2015. Evidence of a community shift early in the time series is supported by our

404 regime detection analysis, which demonstrated that a two-state model best described the latent

405 trend (LOOIC: one-state = 216.4, two-state = 11.8, three-state = 41.8, Fig. 3). This shift

406 coincides with a strong increase in the abundance of a few species during that period, including

407 eared blacksmelt (*Lipolagus ochotensis*), slender blacksmelt (*Bathylagus pacificus*), northern

408 lampfish (*Stenobrachius leucopsarus*), as well as a rise in northern anchovy (*Engraulis mordax*)

409 abundance prior to the shift (S1 Fig.). Our analysis does not document a shift to a novel

410 community state in response to the recent marine heatwave.

411 While this model provided slight support for heavy-tailed Student-t deviations in the

412 latent trend (S2 Fig.), we did not detect any black swan events in the community state. We note

413 that the community response to two strong El Nino events (1982–1983 and 1997–1998) and to

414 unusually low productivity conditions (2005) in the central CCE appear similar in magnitude and

415 duration to the response to the 2014-2016 marine heatwave, although the directions of the

416 responses were opposite (Fig. 4a). Our regime detection analysis also captured the change in the

417   central CCE community in the mid to late 2000s (Fig. 3), which may be associated with the large

418   changes in the reproductive success of multiple seabirds (e.g., Cassin's auklet, common murre,

419   Brandt's cormorant) and in sea lion pup births around that time (S1 Fig). These taxa may have

420   been impacted by changes in the abundance or availability of important prey items resulting from

421   unproductive ocean conditions in the central CCE in 2005 and the below normal SSTs associated

422   with the 2007-2008 La Nina Event (McClatchie et al. 2008, 2009, Bjorkstedt et al. 2010).

423

424   *Forecast of community state*

425   In comparing models of the biological response with and without climate covariates, we found

426   that several biology models with climate predictors outperformed the biology models that did not

427   include covariates (S2 Table). The climate covariate resulting in the best future predictions of

428   community state was BEUTI (central region), followed by CUTI (central region) (Table 2, see

429   S2 Table for all models). The coefficients linking BEUTI to observed time series (**B** matrix)

430   indicate strong, positive relationships between nitrate flux and the reproductive success of

431   seabirds and the abundance of krill in the central California Current (Fig. 5). They also indicate

432   strong, negative relationships between nitrate flux and the abundance of juvenile/adult Pacific

433   sardine and larval northern anchovy (Fig. 5). The remaining biology-BEUTI relationships were

434   moderate (e.g., ichthyoplankton, market squid *Doryteuthis opalescens*) to weak (e.g., rockfish

435   spp., Fig. 5). The biology-CUTI model was similar to the biology-BEUTI model with respect to

436   model structure and estimated species loadings. The estimated coefficients in the CUTI model

437   also show a similar pattern to those in the biology-BEUTI model (S5 Fig.). The remaining

438   covariate models only showed weak climate-biology relationships (e.g., S5-S6 Fig.).

439

440 **Table 2**. Summary information for the top biology-covariate Bayesian DFA models for each

441 covariate and the top two biology only models (years 1981-2017). The table indicates whether

442 process error was estimated ('Yes') or fixed ('No'), the number of model trends, expected log

443 pointwise predictive densities (ELPD), standard error of ELPD, the environmental covariate

444 included in the model, and the region in the California Current over which the covariate was

445 aggregated. All models had an AR(1) coefficient on the trend and Student-t deviations. Model 1

446 was deemed the best model based on its highest predictive accuracy (highest ELPD value)

447 compared to all other models. BEUTI = Biologically Effective Upwelling Transport Index; BV =

448 Brunt-Väisälä frequency; CUTI = Coastal Upwelling Transport Index; ILD = Isothermal Layer

449 Depth; SST = Sea Surface Temperature; SSH = Sea Surface Height. See S2 table for the full

450 suite of model comparisons.

451

Model	Process sigma	Trends	ELPD	SE ELPD	Covariate	Region
1	**No**	**1**	**-1878.71**	**71.52**	**BEUTI**	**central**
2	No	1	-1905.27	81.98	CUTI	central
3	No	1	-1914.62	83.22	ILD	south
4	No	1	-1927.33	88.26	SST	south
5	No	1	-1928.03	88.39	BV	south
6	No	1	-1946.75	86.33	SSH	south
7	No	1	-1951.44	73.59	None	-
8	Yes	1	-2038.71	91.44	None	-

452
453

454 **Figure 5.** A summary of the effect of the Biologically Effective Upwelling Transport Index

455 (BEUTI), a measure of nitrate flux through the base of the mixed layer, on the single species

456 parameters. Cal. = California, Juv. = juvenile fish stage, Juv./adult = juvenile and adult fish

457 stages combined, all other fish are larval fish. Blue error bars reflect 95% credible intervals.

458 Figures S4-S6 show effects of other environment covariates on the biological variables.

459

460   Given that the biology-BEUTI model was the best supported model over the null model

461   (a model without covariates), we were interested in evaluating the ability of this covariate model

462   to forecast the community state. Comparisons between the community state (out-of-sample

463   estimates) and the community state forecasts indicate that we had skill in forecasting community

464   state one year in advance (Fig. 6, S7 Fig., S8 Fig.). Forecasts of the community trend values for

465   nine additional years (2009–2017, S8 Fig.) also indicate that we had some skill for many of the

466   years tested. There are wide confidence intervals around the forecasts; however, given our

467   methodology we can expect that the credible intervals around the trend forecast will be larger

468   than the historical credible intervals (Fig. 6). Forecasts have more uncertainty than historical

469   values because the variance of a random walk increases linearly with time (Holmes 2004; Ward

470   et al. 2014). Furthermore, our credible intervals are increased because we are additionally (1)

471   propagating full parameter uncertainty across the MCMC draws projecting it, and (2) using a

472   Student-t distribution, which has heavy tails and therefore makes the uncertainty intervals wider

473   than if we used normal distribution.

474

475   **Figure 6.** Community variability and forecast of the community state in the southern California

476   Current. The shared biology trend (blue line, with 95% credible intervals) derived from biology-

477   BEUTI model fit to subset of data (1981–2018) is shown along with the trend forecast for 2018

478   (circle, with 95% credible intervals). See S7 Fig. for model loadings.

479

480   Overall, the model forecast skill of individual species parameters was moderate to high

481   for half of the species included in the biology-BEUTI model (S3 Table, S9 Fig.). It is important

482   to emphasize that the source of variability in predictions for each of the original time series is a

483   mixture of the magnitude and uncertainty around the trends and loadings (x_t, $\mathbf{Z}$), and the

484   magnitude and uncertainty in the estimated covariates ($\boldsymbol{b}$). On the one hand, the time series

485   associated with the highest predictive skill (i.e., lowest prediction errors) included seabird

486   reproductive success (Common murre *Uria aalge*, Cassin's auklet *Ptychoramphus aleuticus*) and

487   the abundance of juvenile Pacific sanddab *Citharichthys sordidus*, juvenile halfbanded rockfish

488   *Sebastes semicinctus*, market squid, and several ichthyoplankton species (S3 Table, S9 Fig.). On

489   the other hand, forecast skill was lowest (i.e., highest prediction errors) for the abundance of

490   some juvenile rockfishes (chilipepper *Sebastes goodei* and widow rockfish *Sebastes entomelas*)

491   and larval fishes (northern anchovy, mesopelagics), which is likely attributed to a lag or

492   mismatch in the timing of the climate-biology relationships. These patterns in forecast skill are

493   similar to those based on the biology-CUTI, -SST, and -ILD models (S3 Table). Lastly, the

494   uncertainty around model predictions of species parameters appears to be driven more by the

495   precision of the model coefficients than by the loadings on the community trend (e.g., S10 Fig.).

496

497   **Discussion**

498   We applied a novel set of statistical tools to data from the southern and central regions of the

499   CCE to document the community response to climate perturbations over the past six decades and

500   to create near-term forecasts of community state. Our analysis detected a community response to

501   the 2014-2016 northeast Pacific marine heatwave; however, it did not exceed normal variability

502   within the study timeframe or result in a shift to a novel community state, based on the biological

503   time series investigated here. We identified relationships between community state and multiple

504   climate variables, with nitrate flux through the base of the mixed layer having the strongest

505   correspondence with individual species time series and the shared trend in community

506   variability. Moreover, we demonstrated skill in creating simultaneous one-year lead time

507   forecasts of species responses and community state.

508   There have been several studies and anecdotal evidence of unexpected biological

509   responses to the 2014–2016 northeast Pacific marine heatwave. Based on the biological time

510   series included in our analysis, the broader CCE community demonstrated a response to the

511   marine heatwave, i.e. the biology trend is higher over those years than in previous years.

512   However, our results do not demonstrate a widespread community reorganization beyond the

513   archetypal community structure of this recognizably dynamic ecosystem within the southern and

514   central CCE in response to this event. Instead, the mean values for the shared trend in the

515   biology time series, as well as for the shared climate trend, were within the range of previous

516   observations. An unusual aspect of the 2014–2016 events, relative to past warming associated

517   with El Niño or other low-productivity warm periods, was the very high abundance of young-of-

518   year rockfish and anchovy (Santora et al. 2017, Thompson et al. 2019, Schroeder et al. 2019),

519   which differed from most past warm events in which the abundance of these taxa was greatly

520   reduced. There were many species present during the marine heatwave that are not typically

521   observed in sampling or associated with the CCE, but those exceptional presences and high

522   abundances of warm species did not result in a persistent signal among the species for which we

523   have time series contributing to the DFAs. While our study did not detect a shift in community

524   state in the southern and central CCE during the 2014–2016 heatwave, we did detect a shift in

525   the 1960s. The 1960s shift was likely due to a regime shift previously detected in the southern

526   California ichthyoplankton community (Peabody et al. 2018); the southern California

527   ichthyoplankton time series are the only data used in our analysis that pre-date the 1970s.

23

528   Peabody et al. (2008) identified several species that caused the 1960s shift and their study

529   included a much broader suite of ichthyoplankton species than our study which limits our ability

530   to evaluate whether the species driving the shifts are consistent among studies. Previous studies

531   also documented a shift in response to the 1977/1978 PDO shift (e.g., McGowan et al. 2003,

532   Peabody et al. 2018) while our analyses did not. Our estimated biology trend is consistent with

533   the evidence of this regime shift, however, only ichthyoplankton time series are available prior to

534   the 1970s and there are gaps in the ichthyoplankton data between the late 1960s through the

535   1970s (CalCOFI only sampled every third year during this time). The trend estimate therefore

536   has higher uncertainty during this period than elsewhere in the time series. This likely limits any

537   detection of a regime shift in the mid to late 1970s. In a recent study, Litzow et al. (2020a)

538   applied Bayesian DFA to 11 climate time series and 48 biology time series in the Gulf of Alaska

539   (GOA). While their study revealed markedly elevated values in a shared climate trend between

540   2014–2019, it did not provide evidence of a shift to a novel mean state in shared trends of

541   ecosystem variability during the extreme warming event. Their analysis did, however, capture

542   the rapid community change in the GOA following the 1970's PDO shift in the northeast Pacific

543   Ocean. We note that our study, as well as Litzow et al. (2020a), are based on time series that

544   only extend a few years beyond the heatwave. As additional years of data become available, the

545   CCE and GOA Bayesian DFA models could reveal different outcomes. However, this is unlikely

546   given that the taxa and life stages used in both studies are known to respond quickly to changes

547   in ocean conditions, i.e., within less than one year, and given our assumption that the surveys are

548   consistently sampling at the right time and location to fully characterize the short-term response.

549   A compelling outcome of our analysis and the similar analysis of Alaskan species by

550   Litzow et al. (2020a) is that neither detected state changes in North Pacific communities

551   following the massive 2014-2016 marine heatwave, despite the extremely anomalous physical

552   conditions throughout most of the basin and a litany of concurrent biological, ecological, social

553   and economic effects (see Introduction). An important characteristic of both studies is the

554   temporal scale of community analysis (1972-2017 for the GOA and 1951-2017 for the CCE).

555   This long temporal scale provides an important context for comparing contemporary change with

556   the magnitude of historical community shifts. In addition, the Bayesian DFA accounts for

557   uncertainty in the shared trends in a way that prevents premature detection of wholesale

558   ecosystem shifts. We note that Suryan et al. (2021), fitted a single-trend, non-Bayesian DFA

559   model to a larger set of GOA biological time series ($n = 187$) over a shorter time span (2010-

560   2018) and found evidence of a well-resolved shift that implied different community states during

561   2010-2014 and 2015-2018. The different conclusions of Suryan et al. (2021) and Litzow et al.

562   (2020a) studies speak to an inherent tension in retrospective analyses of community change.

563   Limited time series availability means that analyses can be taxonomically and functionally broad

564   (e.g., Suryan et al. 2021), or temporally extensive (e.g., Litzow et al. 2020a), but not both. Each

565   approach has advantages, but direct comparison between the two is difficult. Given the impacts

566   of the 2014-2016 event, and that long-term warming combined with marine heatwaves will push

567   the CCE into novel climate states, we must consider ecological mechanisms that might explain

568   why these communities were apparently resilient to the marine heatwave, along with revisiting

569   methodological details that could further clarify our results.

570   The CCE shared biology trend and loadings captured unexpected patterns in the

571   community response to regional climate perturbations. The biology time series included in this

572   study showed strong coherence in community signal in response to regional climate

573   perturbations across multiple trophic levels, life-history strategies, and datasets. Most of the

574　biological time series loaded in the same direction on the shared trend, with only a few time

575　series showing the opposite pattern. In addition, several species that are typically associated with

576　cooler ocean conditions show increased relative abundances during the marine heatwave. For

577　example, past studies have shown that high abundances of pelagic juvenile rockfish and

578　groundfish, squid, and krill are associated with more southward transport in the California

579　Current, and more subarctic source waters, with abundance far lower in years with more

580　subtropical waters, which are often associated with El Niño and anomalous warm events

581　(Ralston et al. 2015, Schroeder et al. 2019). Our analysis captured this documented pattern,

582　showing a reduced abundance of these species that have been associated with subarctic source

583　waters and strong equatorward flow in the California Current during two of the strongest El Nino

584　events on record (1982–1983, 1997–1998) and unusually low productivity conditions (2005–

585　2006, Peterson et al. 2006). Our analysis also captured the unexpected increase in abundance of

586　these taxa in 2014–2016 despite the anomalously warm ocean conditions at that time. This may

587　be partially explained by the observation that subsurface waters were more subarctic, rather than

588　subtropical in origin (Schroeder et al. 2019) and that there was some strong upwelling during the

589　marine heatwave, particularly in spring 2015 (Peterson et al. 2015, Ryan et al. 2017). The

590　reduced production of juvenile/adult Pacific sardine and increase in juvenile northern anchovy

591　between 2014 and 2016 shown here and elsewhere (Thompson et al. 2019) were consistent with

592　a history of observations indicating that these species tend to respond asynchronously to ocean

593　conditions (MacCall 1996, Schwartzlose et al. 1999, Chavez et al. 2003, Deyle et al. 2013,

594　Sydeman et al. 2020). However, the responses were of opposite sign from past observations of

595　increases in sardines and decreases in anchovy under warm conditions (Chavez et al. 2003). The

596　DFA trends and loadings indicate a negative response of sea lion pup growth and weight to the

597   2014–2016 marine heatwave, which also aligns with past work showing that reduced prey

598   availability for nursing mother sea lions is unfavorable for sea lion pups (McClatchie et al.

599   2016). Notably, sea lion pup condition covaried with abundance of anchovy and sardine, which

600   provide quality prey to sustain lactation. Pup condition also improved at the tail end of the

601   marine heatwave when, despite the warm water, anchovy abundance increased dramatically and

602   by 2017 all metrics of pup condition were above average (Thompson et al. 2019). In addition,

603   the trends and loadings suggest that the reproductive success of some seabirds in the central

604   region of the CCE was not diminished by the heatwave, although recent studies have

605   documented the severe impact of the heatwave on seabird productivity in regions to the north

606   (Piatt et al. 2020). Our analysis is not able to capture the irruptions of fishes and invertebrates

607   that are rare in long-term CCE time series. Many sporadically occurring taxa such as pelagic red

608   crabs (*Pleuroncodes planipes*), which are absent from California waters in most years but

609   abundant infrequently in warm years with anomalous transport from the south, are not well

610   suited to include as time series due to large number of zero observations in the survey data.

611   Incorporating climate information in DFA models of CCE biology indicated that models

612   with a climate covariate performed better than models without one. The model results suggest

613   that nitrate flux into the surface mixed layer (BEUTI) was the best covariate for individual

614   species in addition to the shared trend in the southern and central CCE over the past three

615   decades. Nitrate flux had a strong positive effect on the abundance of krill and some larval fishes

616   and on the reproductive success of seabirds, and a moderate positive effect on some pelagic

617   juvenile fishes, squid, and sea lion pup births. Stronger upwelling magnitude (CUTI), which is

618   correlated with nitrate flux, was the second-best predictor of community variability and had a

619   positive albeit weaker effect on the same suite of species (S4 Fig.). These findings are consistent

620   with mechanistic understanding as upwelling increases the supply of nutrients from deep to

621   shallow waters and enhances the productivity at the lower trophic levels that affect foraging

622   conditions for higher trophic level species in coastal habitats. For example, past work has shown

623   that rockfish abundance is positively associated with upwelling strength (Ralston et al. 2013),

624   and seabird productivity has been shown to increase when ocean conditions support high primary

625   production and higher trophic level prey (e.g. Wells et al. 2008). Rockfish production is also

626   higher when subsurface source waters in the California Current are more subarctic rather than

627   subtropical, which may explain the negative effect of isothermal layer depth (ILD) and

628   temperature on some rockfish species (S5 Fig., S6 Fig.). More subtropical source waters and

629   surface warming tend to be associated with deeper isopycnals, higher stratification, and

630   shallower ILD (Schroeder et al. 2019, Bograd et al. 2019). Nitrate flux (BEUTI) had a strong

631   negative correlation with juvenile/adult Pacific sardine and larval northern anchovy and

632   upwelling strength (CUTI) did as well. The relative abundance of Pacific sardine in coastal

633   waters off of Central California has been shown to be lower during periods of strong upwelling

634   (Santora et al. 2014, Ralston et al. 2015). This trend may reflect a change in the production of

635   Pacific sardine or a shift in their relative distribution. In addition, a negative relationship between

636   upwelling and nitrate flux and sardine recruitment can generally be explained by the transfer of

637   fish larvae to offshore areas where they have low chance of survival during periods of strong

638   equatorward flow and upwelling (Bailey and Francis 1985, Nieto et al. 2014), although our

639   understanding of the mechanisms driving anchovy population dynamics is limited (Sydeman et

640   al. 2020). We acknowledge that climate drivers often act in concert to influence community

641   variability, and here we are evaluating the effects of the climate variables one at a time. An

642   important next step of this work will be to examine whether including multiple climate

643   covariates in the CCE biology model further improves the forecast skill of the model and our

644   community state indicator. However, the individual climate variables are collinear and share

645   information, which affects our ability to makes inference on the covariates. Furthermore, our

646   study is an attempt to synthesize a broader suite of community indicators and their response to

647   climate perturbations and therefore should not be interpreted as replacing or simplifying more

648   detailed investigations into the drivers and mechanistic understanding of the indicators included

649   here.

650   Our approach for creating simultaneous predictions of species responses and shared

651   ecosystem variability to ocean conditions shows promise for developing near-term forecasts of

652   community state. Our forecasts are based on ocean model data derived from the CCE ROMS,

653   which have been applied in several recent studies to examine how oceanographic processes

654   affect fish recruitment variability (Tolimieri et al. 2018, Haltuch et al. 2020) and productivity

655   (Siegelman-Charbit et al. 2016), species habitat suitability (Abrahms et al. 2018, Cimino et al.

656   2020), and species spatial distributions (Muhling et al. 2019, 2020). The CCE ROMS also

657   supports nowcasts of species distributions based on observed ocean conditions that can help

658   resource managers and users manage risks associated with fisheries bycatch and ship-strike

659   (Hazen et al. 2017, 2018, Welch et al. 2019). Moreover, multiple efforts are underway in the

660   CCE and other coastal systems to develop short-term forecasts (1–24 months) of ocean

661   conditions for uptake by scientists, managers, and other end-users (Siedlecki et al. 2016, Kaplan

662   et al. 2016, Jacox et al. 2020, Malick et al. 2020). Here, we were able to create forecasts of

663   community state and several individual species parameters one year in advance based on

664   observations of a single climate variable (nitrate flux). The lead-time of such a forecast could be

665   extended further by using forecasts of ocean conditions rather than observed conditions, and

666 ocean temperatures in the CCE can be skillfully forecast months to a year in advance, with

667 particularly high skill in the late winter and spring (Jacox et al. 2019). As mentioned above,

668 future extensions of our work will evaluate whether a combination of climate variables as well as

669 time lags might improve our forecasting skill.

670   In the CCE, nonstationary relationships are an important consideration for producing

671 reliable ecological forecasts in this ecosystem. While the year-to-year variability in the estimated

672 trend did appear to be stationary for our community models (Fig. 4, 6), the autocorrelation

673 appeared to be nonstationary with the lag-1 autocorrelation between 2000–present being

674 significantly higher (0.82) than over the years 1981–2000 (0.23). In addition to nonstationary

675 variance parameters, future analyses may also consider nonstationary relationships in the

676 covariate relationships, or potential interactions between covariates. A growing number of

677 retrospective analyses have revealed nonstationary relationships among climate and individual

678 species or community-level variables (Puerta et al. 2019, Litzow et al. 2018, 2019, 2020 a,b,c).

679 In the northeast Pacific Ocean, these studies have been mostly focused on Alaskan ecosystems,

680 which have long time series that support robust statistical analysis of nonstationarity in climate

681 and biological systems. The best-documented instance of nonstationary relationships among

682 climate and biology time series in the North Pacific centers on a climate shift in the late 1980s

683 (Litzow et al. 2020b). Decades of observational data on either side of that event allow for

684 statistically robust tests for nonstationarity that are not yet available for post-2014–2016

685 conditions. The problem of having few years of available data is an inescapable limitation for

686 evaluating the possibility that nonstationary relationships might accompany emerging, novel

687 climate conditions. Similarly, the considerable historical and paleoceanographic evidence for low

688 frequency variability in the productivity of many key marine populations, particularly coastal

689   pelagic species such as Pacific sardine and northern anchovy, also complicates the challenges

690   associated with detecting nonstationarity with data of a limited temporal duration (Baumgartner

691   et al. 1992, MacCall 1996, Field et al. 2009), although such patterns may lead to greater risk of

692   "detecting" nonstationarity when in fact it may not exist (Cohn and Lins 2005, Milly et al. 2015).

693   However, early indications from Alaska suggest the possibility that long-standing relationships

694   between leading climate modes and individual climate and biology time series may have

695   changed following 2014 (Litzow et al. 2020c).

696   Using DFA to forecast attributes of community structure in the CCE allows us to create

697   simultaneous forecasts of trends, or 'ecosystem state', and raw time series. This approach could

698   also be applied individually to each dataset in our analysis to generate taxa-specific indicators

699   (e.g., seabird productivity, juvenile fish abundance), though forecasts would be expected to differ

700   from those with the entire CCE data. Similarly, if ecosystem states were not a focus of inference,

701   alternative forecast models could be applied (e.g., ARIMA or non-parametric models, Ward et al.

702   2014). Forecasts for individual time series from the DFA models used here can be seen as a

703   mixture of the AR forecast on the estimated trends (Fig. 6), and linear effects of forecasted

704   climate variables on each time series (Fig. 5). Species that have strong associations or loadings

705   on the trend and estimated climate effects that are large in magnitude (e.g., market squid, Pacific

706   sanddabs, shortbelly rockfish *Sebastes jordani*) are expected to have the most accurate

707   predictions, while those species with weak loadings and weaker effects of climate variables (e.g.,

708   California smoothtongue (*Leuroglossus stilbius*) are expected to have worse forecast

709   performance.

710   Our approach for developing a community state indicator to track and predict the

711   response of marine ecosystems to climate perturbations has the potential to support ecosystem-

712 based and climate-ready management in multiple ways. Garnering knowledge of community

713 state and the potential for large shifts in ecosystem structure in response to intense and novel

714 climate perturbations can help inform better, more rapid management decisions for mitigating

715 ecological and socioeconomic impacts. The combination of long-term monitoring surveys and

716 data with the modeling framework we advance here can also help scientists identify or refine key

717 variables of ecosystem change that are summarized for ecosystem assessments in support of

718 decision-making (Harvey et al. 2020). For example, it might be prudent to emphasize ecological

719 time series that load strongest on ecosystem state trends and demonstrate strong, predictable

720 relationships with climate variables (or other covariates of interest) over time series with weaker

721 loadings on shared trends of community variability or have low forecast skill with environmental

722 variables. Furthermore, our approach can provide valuable ecosystem information for scientific,

723 management and coastal communities during times when researchers cannot sample the biology

724 in marine ecosystems. This added value became acutely apparent in 2020 when myriad ocean

725 surveys were cancelled or limited in spatiotemporal scope due to safety restrictions associated

726 with the COVID-19 pandemic. Finally, our approach provides a quantitative way to help

727 managers discern short-term periods of unusual community dynamics and/or high variability—

728 such as the 2014-2016 marine heatwave—from state shifts that represent more enduring

729 transitions into new regimes of ecosystem structure or productivity. Given that global climate

730 change is expected to amplify ocean change, approaches like the one applied here will become

731 increasingly valuable for marine resource management and conservation.

732

733 **Acknowledgements**

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747 **References**

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Supporting Information

S1 Appendix: Standardization of time series from spatially resolved datasets.

S1 Table: Climate and biology time series included in the analyses

S2 Table: Summary information for the Bayesian DFA biology-covariate and biology only models (years 1981–2017).

S3 Table: Observations, predictions, and prediction errors for single species parameters in 2018.

S1 Figure: Climate and biology time series used in the study analyses.

S2 Figure: AR(1) coefficient on the southern/central California latent climate trend and support for a heavy-tailed deviations of the latent trend.

S3 Figure: The Student-t deviations degrees of freedom parameter (nu) in the southern/central California biology trend.

S4 Figure: A summary of the effect of the Cumulative Upwelling Transport Index (CUTI) on the individual single species parameter included in the DFA analyses

S5 Figure: A summary of the effect of the Isothermal Layer Depth (ILD) on the individual single species parameter included in the DFA analyses.

S6 Figure: A summary of the effect of the sea surface temperature on the individual single species parameter included in the DFA analyses

S7 Figure: Community variability in the southern California Current ecosystem (1981–2018).

S8 Figure: Forecasts and model estimates of the 'true' community state in the southern and central California Current in years 2009–2018.

S9 Figure: Fitted values for biology-covariate model including BEUTI (nitrate flux) as a covariate (1981–2017).

1055   **S10 Figure**: Log coefficient of variation (CV) of 2018 predictions of individual species

1056   parameters plotted against the mean and log CV of loadings related to each species, and the

1057   mean and log CV of coefficients relating each species to BEUTI (nitrate flux).